REVISION OF THE EXTINCT MACROPODID GENUS STHENURUS OWEN IN QUEENSLAND

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While specimens of *Sthenurus* Owen are not common in Queensland Upper Cainozoic deposits, the genus is moderately well represented in the collections of the Queensland Museum. Much of this material formed the basis for the revision of De Vis (1895), and this has been supplemented by recent collections from the Darling Downs, south-eastern Queensland. A study of all this material together with the relevant literature has enabled results of some taxonomic importance to be presented. Evaluation of the incomplete locality data available supports previous stratigraphic conclusions by Woods (1960b) regarding the possible existence of at least two different sequences within the Upper Cainozoic sediments of the Darling Downs.

The genus *Sthenurus* was proposed by Owen (1873) for *Macropus atlas*, a species described originally by Owen (1838) from the Wellington Caves in New South Wales. *S. brehus*, described by Owen (1874), is now known to be referable to the genus *Protemnodon* Owen. De Vis (1895) recognized the existence of additional species in collections from the Darling Downs and described *S. oreas* and *S. pales*. A further species, *S. occidentalis*, was named by Glauert (1910a) from the Mammoth Cave, Western Australia, while recently Marcus (1962) has described *S. andersoni* from the Pleistocene clay deposits near Bingara, north-eastern New South Wales. Most of the recorded material is from Pleistocene sediments, although one Victorian specimen, referred by Stirton (1957) to the Sthenurinae has been dated by Gill (1953) as Lower Pliocene. Another Tertiary occurrence is the lower incisor referred to the Sthenurinae by Stirton *et al*. (1961), from the Pliocene Mampuwordu Sands at Lake Palankarinna, north-eastern South Australia.

De Vis (1895) amalgamated the genus *Procoptodon* Owen with *Sthenurus*, a union which is no longer tenable in the light of the present conception of the genera. A new subfamily, the Sthenurinae, was proposed by Raven and Gregory (1946) to include, not only *Sthenurus* and *Procoptodon*, but also *Palorchestes* Owen. Tate (1948) treated *Procoptodon* as a subgenus of *Sthenurus*. *Palorchestes* was removed from the Macropodidae by Woods (1958), who showed that its affinities are with the Diprotodontidae. Supporting Simpson (1930, 1945) and earlier workers, Ride (1959) assigned *Procoptodon* to the Macropodinae because of the type of tooth replacement and the basic pattern of the molars. These macropodine features, as noted by Woods (1960a), are also present in *Sthenurus*.

The author wishes to express his appreciation to Mr. J. T. Woods of the Queensland Museum for his assistance, to Dr. J. W. Evans of the Australian Museum, Sydney, for the loan of material, and to Mr. W. Dunmall of Dalby, for the donation of recently collected specimens from Pilton, on the Darling Downs.

Measurements throughout are in millimetres.

Family **MACROPODIDAE**

Subfamily **MACROPODINAE**

Genus **STHENURUS** Owen

Sthenurus Owen, 1873, Proc. Roy. Soc. Lon., 21, p. 128; Owen, 1874, Phil. Trans., 164, pp. 265–274.

Type Species.—*Macropus atlas* Owen.

Diagnosis.—Mandible with I_1 spatulate; P_3 elongate, moderately strongly ridged and tuberculate, with prominent lingual crest between paraconid and metaconid, and postero-labial crest associated with protoconid. Molars with broad rectilinear lophids, with oblique ridges descending anteriorly from cuspids; links descending lingual to and below levels of protoconid and hypoconid; ornamentation never exceptionally coarse, and less so on posterior surfaces of lophids; breadth across trigonid basin reduced; talonid basin centrally elevated; lateral surfaces of lophids weakly to moderately convex in anterior view. Maxilla with P^3 elongate, moderately strongly ornamented. Molars with broad, slightly anteriorly bowed, sharp lophs; ornamentation never exceptionally coarse, labially with well developed ridges from paracone and metacone; median valley centrally and labially elevated; metaloph posteriorly with broad fossette.

It has often been noted that *Sthenurus* and *Procoptodon* exhibit extreme shortening, deepening, and increased massiveness of the crania and jaws. However, as indicated by Marcus (1962), the Pleistocene species of *Sthenurus* are divisible into short-jawed forms, somewhat resembling *Procoptodon*, and relatively long-jawed forms. This distinction becomes more obscure with specimens from the presumably older Chinchilla Sand. In the short-jawed members of the genus, the characters approximating to those of *Procoptodon* include the increased lateral convexity of the longitudinal axis of the ramus, the corresponding increase in the thickness of the ramus, and the firmly ankylosed symphysis.

Although basic tooth structure is similar in both genera, many points of difference are readily apparent. In *Sthenurus* I_1 is relatively larger and much more spatulate ; P_3 is relatively longer ; the lower molars are comparatively broader, with more rectilinear lophid crests, but with a narrower trigonid basin, and the labial tooth surfaces are convex in anterior view rather than perpendicular or convergent towards the crests as in *Procoptodon*. Ornamentation in *Procoptodon* is generally extremely coarse, although fewer ridges may be developed on the protolophid surfaces. While the posterior surface of the hypolophid in *Sthenurus* is relatively smooth, that in *Procoptodon* is characterized by coarse vertical ridging. In *Procoptodon* the central portion of the talonid basin is not elevated.

The upper dentition is similarly distinct in *Sthenurus*, with P^3 being comparatively more elongate ; the upper molars are less ornamented, with the lophs less strongly anteriorly bowed and with somewhat broader, sharper crests. The central and labial portions of the median valley in *Procoptodon* are not markedly elevated, while the metaloph has a relatively narrower posterior fossette.

The suggestion of Tate (1948) that *Procoptodon* and *Sthenurus* are related genera cannot be denied, and further it appears likely that *Procoptodon* has been derived from a primitive *Sthenurus* stock. As *Procoptodon* has not yet been located in the Chinchilla Sand or other Pliocene sediments in Australia, it also seems likely it was a rapidly evolving genus, derived late in the geological history of the group. Both genera are well represented in the Pleistocene fluviatile deposits of the Darling Downs.

STHENURUS ANDERSONI Marcus

(Figures 1–3)

Sthenurus oreas De Vis (*partim*), 1895, Proc. Linn. Soc. N.S.W., 10 (n.s.), pp. 96–97.

Sthenurus atlas De Vis (*partim*), 1895, Proc. Linn. Soc. N.S.W., 10 (n.s.), pp. 97–99, pl. 16, figs. 9–10.

Sthenurus andersoni Marcus, 1962, Rec. Aust. Mus., 15, pp. 209–304, fig. 1.

MATERIAL.—Referred specimens in the collections of the Queensland Museum are as follows : F. 2970, partial left mandibular ramus with P_3–M_4, Gowrie, Darling Downs ; F. 2971, partial left mandibular ramus with P_3–M_4, Darling Downs (figd. in part, De Vis, 1895, pl. 16, fig. 10) ; F. 3809, partial left mandibular ramus with M_4, Darling Downs ; F. 3810, partial right mandibular ramus with P_3–M_3, Darling Downs ; F. 3811, partial right mandibular ramus with P_3–M_3, Darling Downs ;

F.3812, partial left mandibular ramus with M_2–M_4, Darling Downs; F. 3813, partial left mandibular ramus with I_1 (incomplete), P_2–M_3, juvenile, Kings Creek, Pilton, Darling Downs; F. 2978, partial right maxilla with M^2–M^3, Darling Downs. (The original of De Vis (1895, pl. 16, fig. 9) is not extant in the Queensland Museum collections).

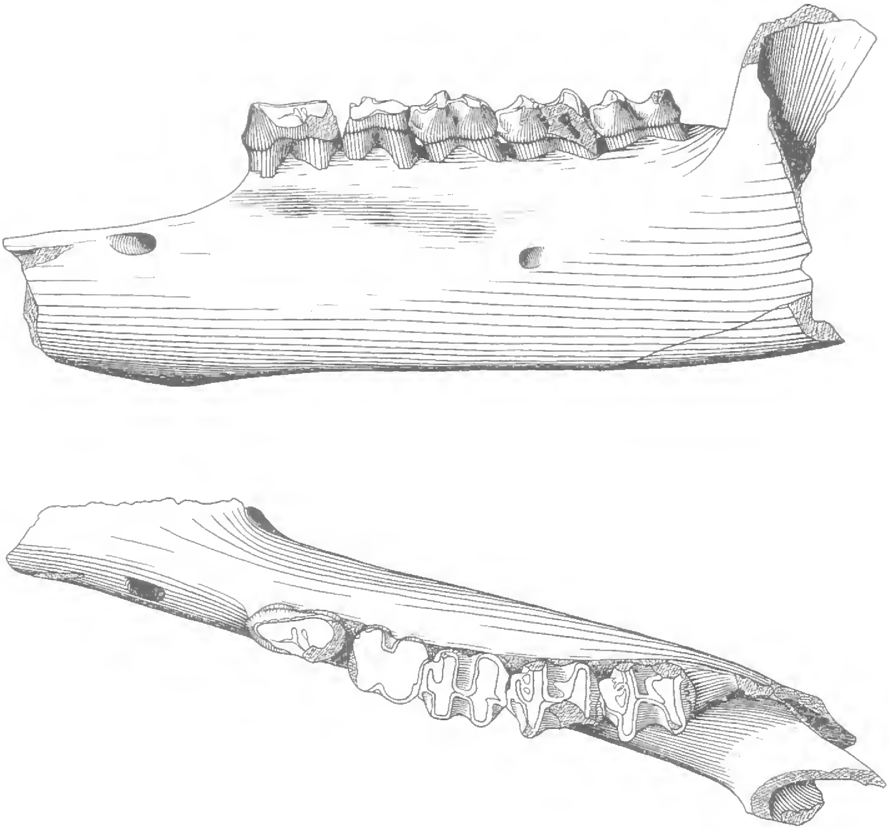


Figure 1.—*Sthenurus andersoni* Marcus. Lateral and occlusal views of incomplete mandible; F. 2970, natural size.

Diagnosis.—Moderately small, long-jawed; P_3 comparatively elongate, narrow, with the median groove at anterior end of postero-labial crest inconspicuous. Lower molars comparatively small; with lophids low, weakly ornamented on anterior surfaces; trigonid basin very narrow. Upper molars comparatively small, weakly ornamented.

Measurements

Mandible

Specimen	P_2	DP_3	P_3	M_1	M_2	M_3	M_4	Mandible depth and width below M_2–M_3
Holotype, Aust. Mus. MF. 946, (Marcus, 1962)	—	—	15·7 x 7·6	—	13·8 x 10·2	14·3 x 11·3	12·7 x 11·1	30·3 x 15·4
Range in Bingara material (Marcus, 1962)	—	—	14·4 – 16·3 x 6·6 – 7·6	11·4 – 11·9 x 8·2 – 8·9	12·5 – 13·8 x 9·6 – 10·2	12·6 – 14·3 x 10·8 – 11·4	12·7 – 13·5 x 10·6 – 11·3	26·4 – 30·3 x 13·0 – 15·4
F. 2970	—	—	—	— x 8·9	12·3 x 9·6	13·2 x —	12·9 x —	28·1 x 14·1
F. 2971	—	—	— x 6·9	—	12·4 x —	13·5 x —	12·5 x 10·7	28·1 x 14·5
F. 3809	—	—	—	—	—	—	13·0 x —	—
F. 3810	—	—	— x 7·1	10·9 x —	13·6 x —	14·3 x 10·8	—	—
F. 3811	—	—	15·2 x 6·8	11·9 x 8·7	13·6 x 9·8	14·4 x —	—	30·9 x —
F. 3812	—	—	—	—	12·2 x 9·6	13·0 x 10·8	12·3 x 10·8	—
F. 3813	7·6 x 5·0	12·2 x 6·6	14·2 x —	11·3 x 7·9	12·6 x 9·0	— x 10·4	—	21·9 x 13·0

Maxilla

Specimen	M^1	M^2	M^3
Univ. of Calif. UC. 60008, (Marcus, 1962) ..	11·0 x 11·2	13·0 x 12·8	—
Aust. Mus. F. 49662. (Marcus, 1962)	—	—	13·6 x 13·0
F. 2978	—	12·9 x —	13·7 x 12·9

Supplementary Description.—P_2 small, subovate in basal outline, anteriorly with small cuspule at basal margin; crown slightly constricted mesially; lingual crest transected by three sets of vertical ridges; curved postero-labial crest flanked anteriorly by inconspicuous groove; intervening basin moderately deep, ornamented.

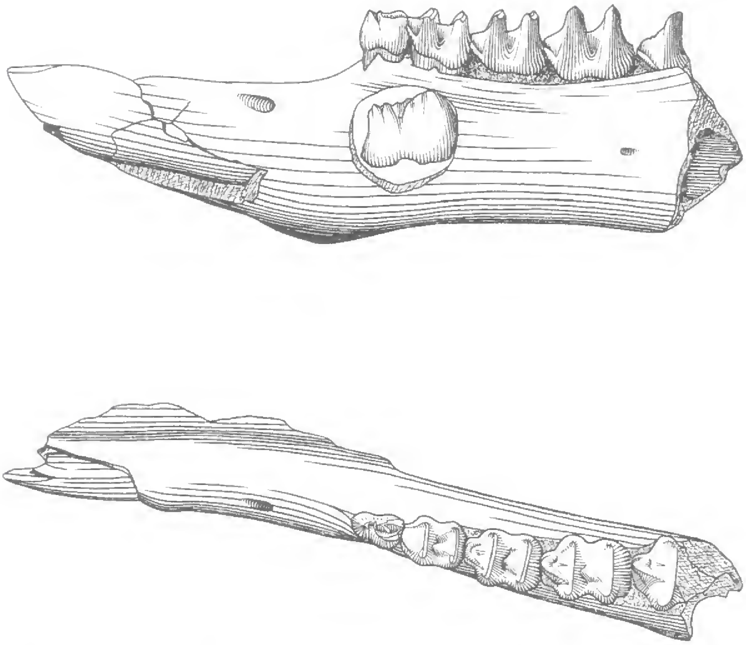


Figure 2.—*Sthenurus andersoni* Marcus. Lateral and occlusal views of juvenile mandible, with unerupted P_3 exposed by fenestration of the ramus; F. 3813, natural size.

DP_3 molariform, subrectangular in basal outline, constricted across talonid basin, with high rectilinear lophids; hypolophid broader than protolophid. Trigonid basin narrow, its length approximately three-fourths distance between lophids; forelink low, descending from near protoconid anteriorly to near mid-point of anterior margin, turning abruptly lingually as curving transverse ridge above low anterior cingulum ; very weak accessory ridges on anterior surface of protolophid. Hypolophid with mid-link strong, descending across elevated central portion of talonid basin from near hypoconid to point labial to mid-point of posterior surface of protolophid ; accessory ornament of strong oblique ridge from entoconid ; posterior surface very finely grooved. Posterior cingulum ill-defined.

The present specimens are morphologically in general agreement with the original material described by Marcus (1962) from the Pleistocene clay deposits. 15 miles east of Bingara, north-eastern New South Wales. However, in the sizes and proportions of the cheek teeth, the Queensland sample appears to form a more variable assemblage, with measurements falling, in many examples, towards or even slightly outside the observed extremes in the original material. Attrition is directly responsible for many of the apparent discrepancies in lengths. Only in the case of F. 3813 is the variation possibly significant. However, compared with the Bingara material, this specimen is identical in all morphological features, except that the lateral surfaces of the lophids of anterior molars are not so markedly convex in anterior view. P_2 and DP_3, retained in F. 3813, appear to be better preserved than in the Australian Museum specimen, MF. 10, mentioned by Marcus (1962) and enable the presentation of supplementary descriptive matter relating to the former.

There is also some departure in the form of the premolar. In F. 3811 it is much narrower above the anterior root and has the lingual crest transected by a very weakly developed set of vertical labial and lingual ridges near the paraconid, in addition to the four sets typically present. However, Marcus (1962) notes that the cuspules along the lingual crest may be subdivided. As in the Bingara material, P_3 exhibits a basal cingulum-like structure below the paraconid, together with a variably developed cuspule at its anterior extremity.

The specimen figured as *S. atlas* by Owen (1874, pl. 22, figs. 5–8), from the Pleistocene deposits of Queensland, is most probably referable to *S. andersoni* because of the size of the cheek teeth and the structure of the molars. P_3 appears to be basally swollen below the paraconid but its true structure is obscured owing to its intermediate stage of eruption. Another specimen, a partial left maxilla from the Condamine River, Darling Downs, originally listed by Owen (1845) as *Macropus atlas*, and later figured (Owen, 1874, pl. 23, figs. 7–9) as *Protemnodon anak*, is also apparently referable to *S. andersoni*. In the case of the mandibles referred by De Vis (1895) to *S. atlas*, Marcus (1962) was correct in his suggestion that the range in morphology indicates that more than one species of *Sthenurus* is present and further that some of the material belongs to *S. andersoni*. De Vis (1895) included the single maxilla here referred to *S. andersoni* in *S. oreas*. Structurally, the teeth are identical with those described by Marcus (1962) and, as the accompanying table of measurements shows, the dimensions are likewise comparable.

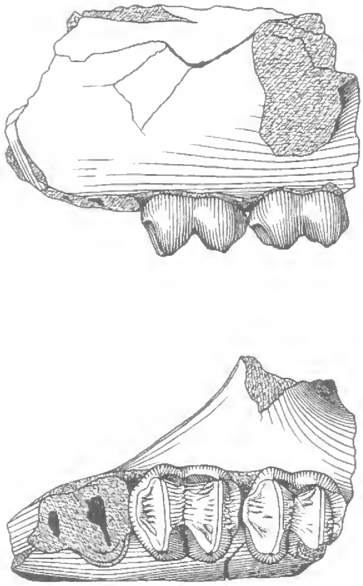


Figure 3.—*Sthenurus andersoni* Marcus. Lateral and occlusal views of maxillary fragment; F. 2978, natural size.

Specimens of *S. andersoni* from Queensland are from scattered localities in the Pleistocene fluviatile deposits of the Darling Downs, whereas the material upon which Marcus (1962) based his description is all from the one locality, Bone Camp Gully, near Bingara, New South Wales. The slight structural and size variations presented by the Queensland specimens may be accounted for in terms of geographical distribution or could be due to slight differences in age between the various localities.

Among the material referred by De Vis (1895) to *S. atlas*, there are two mandibular specimens, F. 813 and F. 814, without locality data, but with preservation suggesting derivation from the Chinchilla Sand. These show close affinity with *S. andersoni*, but are significantly smaller than individuals of this species, and, as well, exhibit some differences in morphological detail. The ramus is shallower, but remains approximately the same thickness as in *S. andersoni* ; all of the cheek teeth are significantly smaller ; P_3 is lower crowned ; and the vertical median groove at the anterior limit of the postero-labial crest is moderately deep and extends towards the crown base. The lower molars are structurally similar to those in *S. andersoni*, but the lateral surfaces of the lophids, when viewed anteriorly, are only very slightly convex. Compared with the partial left mandibular ramus from the Lower Pliocene of Victoria, referred by Stirton (1957) to the Sthenurinae, the lophids in the present specimens are approximately the same width, but the teeth are shorter and have much narrower trigonid basins.

It appears likely, that when better preserved and more accurately localized material from the Chinchilla Sand becomes available, a taxonomic distinction may have to be recognized.

STHENURUS OREAS De Vis

(Figures 4–5)

Sthenurus oreas De Vis (*partim*), 1895, Proc. Linn. Soc. N.S.W., 10 (n.s.), pp. 96–97, pl. 16, figs. 5–6.

MATERIAL.—F. 2923, holotype, associated mandibular rami with all cheek teeth, Darling Downs (figd. in part, De Vis, 1895, pl. 16, figs. 5–6).

F. 3814, partial left maxilla with M^1–M^3, Cement Mills, Gore, S.E. Queensland ; F. 3815, isolated left M^2, no locality.

DIAGNOSIS.—Short-jawed ; ramus very wide, with longitudinal axis slightly convex laterally ; masseteric crest high ; masseteric, mandibular, and mental foramina extremely large. P_3 relatively short, broad, moderately coarsely ornamented. Molars with wide, low, rectilinear lophids, simply but moderately coarsely ornamented on anterior surfaces ; hypolophid with accessory ridge close to mid-link generally well developed ; posterior lophid surfaces weakly ornamented ; trigonid basin moderately wide. Upper molars somewhat coarsely ornamented.

REVISED DESCRIPTION.—Mandible strong, thick, comparatively shallow, with longitudinal axis slightly convex laterally. Symphysis relatively short, ankylosed, at an angle of approximately 40° to base of mandible ; produced postero-ventrally resulting in decided ventral extension of basal margin of ramus below P_3 ; geniohyal pit deep, rather high, well forward of posterior symphysial limit. Diastema short ; ventral margin of ramus broadly rounded between symphysis and diagastric ridge. Mental foramen extremely large, nearly round, antero-ventral to P_3 and close to diastemal crest ; accessory foramen well-defined, halfway between posterior root M_2 and ventral margin of ramus. Ramus with deep labial groove between mental foramen and point below posterior root of M_1. Diagastric process postero-ventral to M_4, moderately developed, separated from base of angle by shallow, post-diagastric sulcus, bounded above by shallow diagastric fossa ; this fossa separated above from shallow depression opening posteriorly into pterygoid fossa. Post-alveolar shelf short, leading to post-alveolar ridge, ascending gradually posteriorly to disappear on mesial wall of coronoid process, immediately above extremely large mandibular foramen. Masseteric crest raised almost to level of occlusion of cheek teeth, with production of an extremely large masseteric foramen ; masseteric fossa deep. Anterior margin of coronoid process inclined beyond vertical.

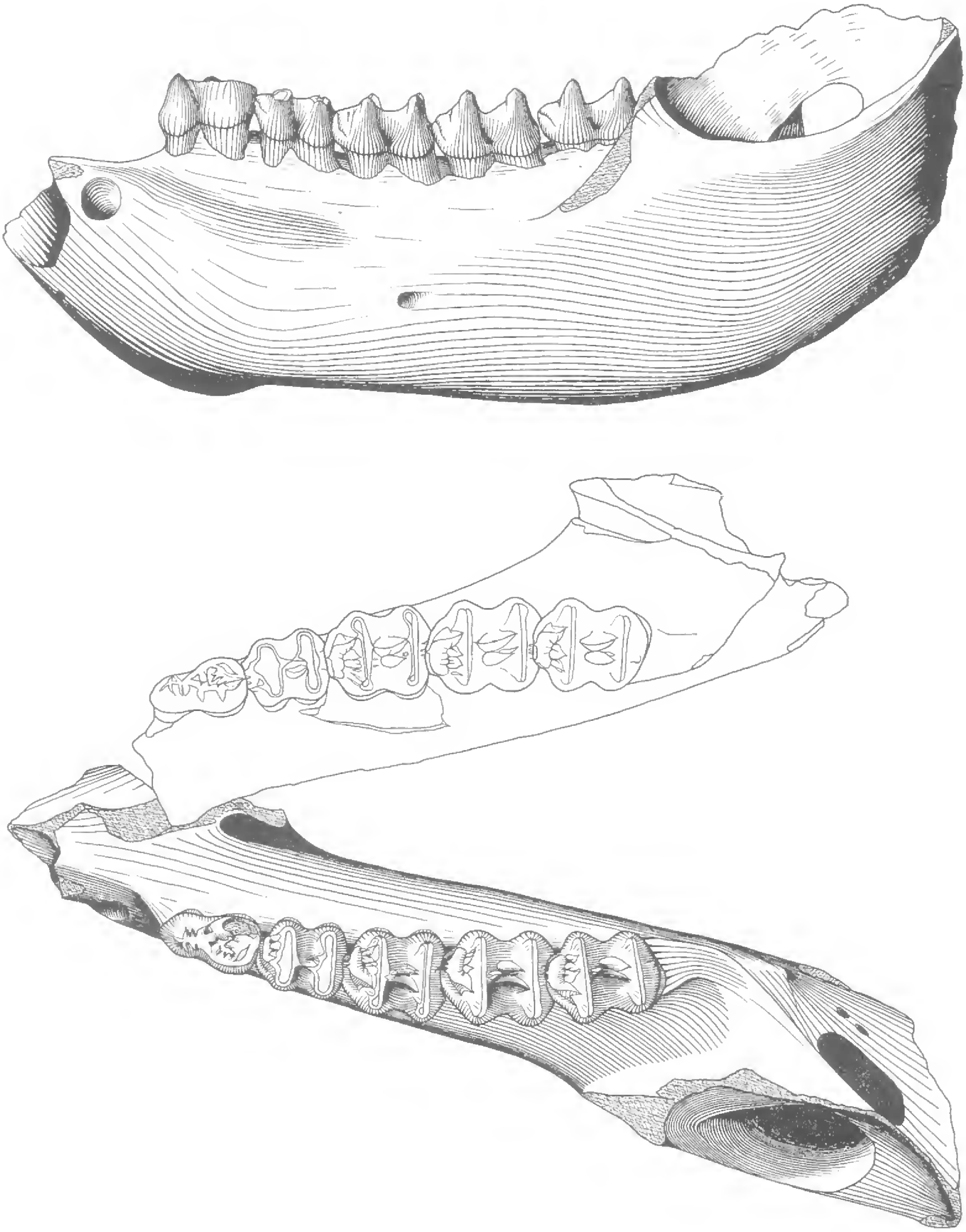


Figure 4.—*Sthenurus oreas* De Vis. Lateral and occlusal views of mandible ; F. 2923, holotype, natural size.

Measurements

Mandible

Specimen	P_3	M_1	M_2	M_3	M_4	Mandible depth and width below M_2–M_3
F. 2923, holotype						
Left ramus	12·3 x —	12·7 x 9·2	14·6 x 10·8	15·8 x 12·0	14·8 x 11·6	30·8 x 20·4
Right ramus	12·6 x 7·5	12·6 x 9·1	14·5 x 10·7	15·5 x 11·7	14·9 x 11·6	31·2 x —

I_1, P_2, and DP_3 unknown, but axes of alveoli of I_1 ascend at approximately 25°.

P_3 relatively short, robust, subtriangular in basal outline. Lingual crest transected by three sets of vertical ridges, with production of cuspules at crest; prominent curved postero-labial crest, flanked anteriorly by broad shallow groove extending almost to base of crown; intervening basin shallow, ornamented by coarse ridges mainly from postero-labial crest.

$M_1 < M_2 < M_3 > M_4$: molars subrectangular, somewhat constricted across talonid basin; lophids relatively low, rectilinear, with hypolophid broader in M_1 and M_2, and with protolophid broader in M_3 and M_4. Trigonid basin relatively broad, its length almost equalling distance between lophids. Forelink low, but strong, descending lingual to and from below level of protoconid, anteriorly to near mid-point of anterior margin, then turning abruptly lingually as transverse ridge above low anterior cingulum; accessory ridges on anterior surface of protolophid strong, few, but variable; oblique ridges from protoconid and metaconid prominent; posterior surface only weakly ridged. Hypolophid with mid-link low, but strong, descending across elevated central portion of talonid basin lingual to and below level of hypoconid to mid-point of posterior surface of protolophid; accessory ornament of oblique ridges from hypoconid and entoconid and generally one relatively strong ridge just lingual to mid-link. Posterior surface finely ridged; posterior cingulum ill-defined.

Measurements

Maxilla

Specimen	M^1	M^2	M^3
F. 3814	12·2 x 11·6	14·1 x 13·1	15·0 x 13·6
F. 3815	—	13·8 x 12·7	—

I^{1-3}, P^2, DP^3, P^3, and M^4 unknown.

$M^1 < M^2 < M^3$; molars subrectangular, slightly constricted across median valley; lophs low, slightly anteriorly bowed; metaloph slightly broader in M^1, protoloph slightly broader in M^2 and M^3. Anterior cingulum relatively low, short, moderately broad, ascending labially, bounded by small style; protoloph anteriorly with slight ridges passing to base of anterior cingulum. Median valley delimited labially by strong ridge descending from paracone, and weaker ridge from metacone. Mid-link rather weak, descending postero-labially then posteriorly from a point labial to and below level of protocone. Enclosed portion of median valley ornamented by relatively coarse, but variable ridges from posterior surface of protoloph and to lesser degree, anterior surface of metaloph. Posteriorly, oblique ridges from hypocone and metacone unite at posterior margin, limiting large, broad posterior fossette, ornamented by coarse vertical ridges from below crest of metaloph.

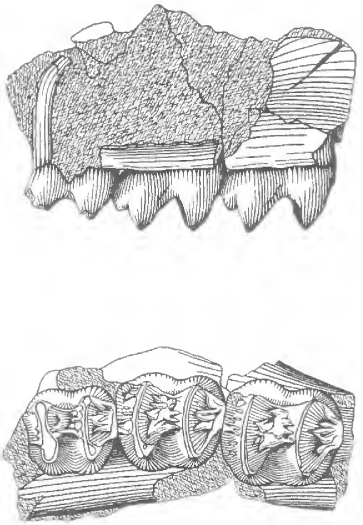


Figure 5. *Sthenurus oreas* De Vis. Lateral and occlusal views of maxillary fragment ; F. 3814, natural size.

Sthenurus oreas, as constituted by De Vis (1895), was a mixture of species, with referred material apparently originating not only from the younger alluvia of the eastern Darling Downs, but also from the Chinchilla Sand. The specific name " *orcas* " which appears in the key of De Vis (1895, p. 89) is considered an orthographic error, elsewhere " *oreas* " is used. The holotype, although not localized, has preservation typical of the Pleistocene sediments. One specimen of De Vis' original series has been referred to *S. andersoni*, and others belong to a new species *S. antiquus* described below. Included in the latter is the specimen (now numbered F. 2931) referred to by Stirton (1957) as the type of *S. oreas*, when he tabulated a series of measurements for forms including this species.

Neither of the maxillary fossils here referred to *S. oreas* was found associated with mandibular remains. The occlusion, however, is satisfactory and the similarity in structure, particularly the moderately coarse nature of the accessory ridging, confirms their relationship.

Compared with the ramus of *S. andersoni*, that of *S. oreas* exhibits conspicuous longitudinal curvature ; the diastema is much shorter ; the symphysis is inclined at a much higher angle ; and the molars are larger and exhibit more intense ornamentation. There is some similarity to *S. occidentalis* Glauert in the structure of the ramus, but this too lacks the longitudinal convexity, and the masseteric crest is raised only to a level slightly below the alveolar margin. In both species, the rami are of approximately the same depth, each has a similarly short diastema, and the symphysial plane and the lower incisors are set at much the same angles. There are, however, great differences in the proportions and ornament of the cheek teeth.

STHENURUS PALES De Vis

(Figures 6–8)

Halmaturus sp. Krefft, 1882, Parl. Pap. N.S.W., 5, pl. 10, fig. 11.

Sthenurus pales De Vis (*partim*), 1895, Proc. Linn. Soc. N.S.W., 10 (n.s.), pp. 94–96, figs. 1–2, 4.

MATERIAL.—F. 815, holotype, isolated right P^3, unworn, Darling Downs (figd. De Vis, 1895, pl. 15, fig. 2).

F. 812, partial right mandibular ramus with P_3 broken at its base, M_1–M_3, adult, ?Ravensthorpe, Pilton, Darling Downs (figd. De Vis, 1895, pl. 15, figs. 1–4). Australian Museum specimen, F. 16489, partial left maxilla with M^2–M^4, Queensland (figd. Krefft, 1882, pl. 10, fig. 11).

DIAGNOSIS.—Extremely large, short-jawed ; mandible thick, and with longitudinal axis slightly curved labially ; diastema short. P^3 very large ; with prominent postero-labial fossette ; high, serrate lingual crest separated from longitudinal crest by deep, relatively coarsely ornamented lingual basin. Lower molars also extremely large, with reduced but numerous accessory ridges ; trigonid basin moderately wide ; mid-link low. Upper molars extremely large, with only very slightly anteriorly bowed lophs and with reduced ornamentation.

Measurements

Mandible

Specimen	M_1	M_2	M_3
F. 812	18·5 x —	21·0 x 17·5	22·4 x —

REVISED DESCRIPTION.—Mandible extremely large, longitudinal axis slightly curved. I_1, P_2, DP_3, P_3, and M_4 unknown, but partial alveolus of I_1 indicates that it was set at moderate angle to base of ramus ; and broken base of P_3 indicates it was quite elongate and broad, corresponding to size of P^3.

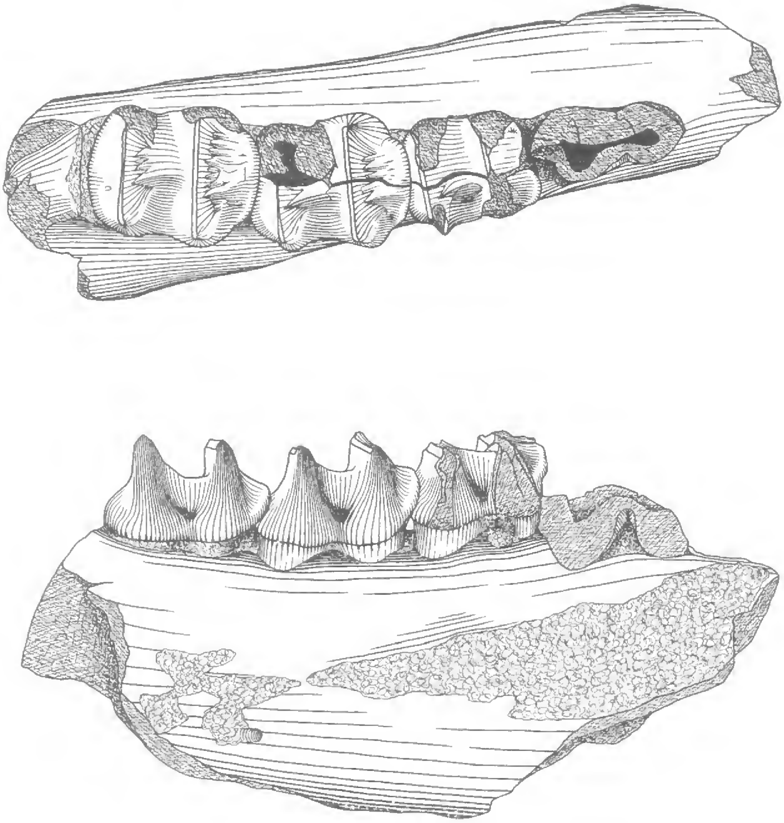


Figure 6.—*Sthenurus pales* De Vis. Occlusal and lateral views of incomplete mandible ; F. 812, natural size.

$M_1 < M_2 < M_3$; molars subrectangular, slightly constricted across talonid basin ; lophids moderately low, rectilinear. Trigonid basin moderately wide, relatively short, its length being approximately four-fifths distance between protolophid and hypolophid. Forelink low, moderately strong, descending lingual to and from below level of protoconid to near mid-point of low anterior cingulum, then turning abruptly lingually as slightly curved transverse ridge, completely obscuring lingual moiety of cingulum ; accessory ridges on anterior surface of protolophid numerous, variable ; also prominent oblique ridges from protoconid and metaconid descending into trigonid basin. Hypolophid with low, moderately strong mid-link across centrally elevated portion of talonid basin lingual to and below level of hypoconid to mid-point of posterior surface of protolophid ; accessory ornament of numerous, variable ridges descending from anterior surface of hypolophid between mid-link and entoconid, accompanied to lesser degree by slight ridges from posterior surface of protolophid ; also oblique ridges from hypoconid and entoconid descending into talonid basin. Posterior surface of hypolophid with faint, vertical ridges. Base of tooth swollen posteriorly, without production of definite posterior cingulum ; slightly elevated mesially.

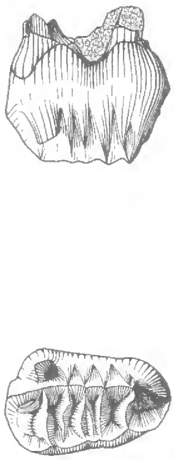
Measurements

Maxilla

Specimen	P^3	M^3	M^4
F. 815, holotype ..	21·9 x 14·1	—	—
Aust. Mus. specimen, F. 16489	—	21·1 x 19·0	19·4 x —

I^{1-3}, P^2, DP^3 and M^1 unknown.

P^3 very large, elongate, broader posteriorly. Crown with high longitudinal crest between paracone and metacone, transected by three sets of vertical ridges with production of cuspules at crest; labial ridges from metacone and adjacent cuspule uniting to form prominent postero-labial fossette. Lower serrate lingual crest joining protocone and hypocone, curving and descending in its anterior and posterior extension; separated from labial crest by deep basin, crossed by several coarse ridges, occasionally bifurcating.



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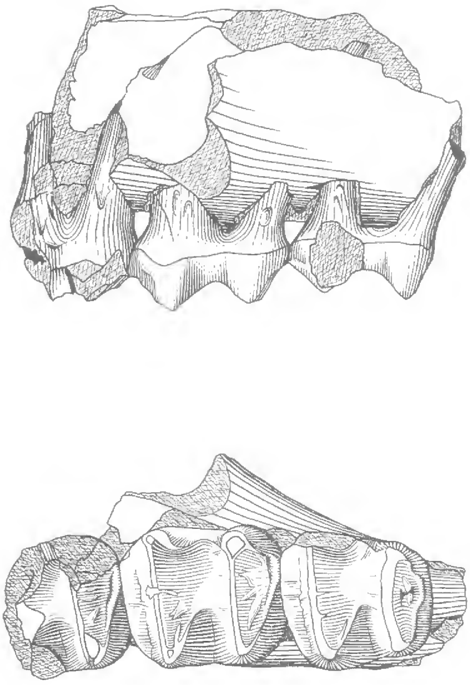

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Figure 7.—*Sthenurus pales* De Vis. Lateral and occlusal views of isolated P^3; F. 815, holotype, natural size.

Figure 8.—*Sthenurus pales* De Vis. Lateral and occlusal views of maxillary fragment; Aust. Mus. specimen, F. 16489, natural size.

$M^2 < M^3 > M^4$; molars subrectangular, slightly constricted across median valley, lophs moderately low, very slightly bowed anteriorly; protoloph slightly broader than metaloph in M^3, much broader in M^4. Anterior cingulum relatively low, short, broad, connected by labial ridge to paracone and by variable ridges to base and anterior surface of protoloph. Median valley labially elevated, delimited by strong, complexly curved ridge descending posteriorly from paracone, and ridge from metacone. Mid-link very low, descending postero-labially then posteriorly from a point, labial to and below level of protocone, to mid-point of metaloph; also postero-labial ridge descending from protocone into median valley. Enclosed portion of median valley ornamented by sparse, slight, but variable ridges from posterior surface of protoloph and to lesser degree, anterior surface of metaloph. Posteriorly oblique ridges from hypocone and metacone unite near posterior tooth margin, limiting large, moderately broad posterior fossette, ornamented particularly in M^2 and M^3 by vertical ridges from below crest of metaloph.

As with *S. oreas*, this species, as constituted by De Vis (1895), was composite. The type lacks locality data, but its preservation is typical of specimens from the Pleistocene fluviatile deposits in the south-eastern Darling Downs. The unworn P_3, figured as *S. pales* by De Vis (1895, pl. 15, fig. 3) is most probably from the Chinchilla Sand. It is now associated as a part of F. 2931, referred to a new species, *S. antiquus*, described below, and is considerably smaller than the size indicated for P_3 of this species by the broken base of this tooth in F. 812. The second isolated P^3 now numbered F. 2972, originally referred to *S. pales* by De Vis, differs in both size and structure from the holotype and appears to be referable to a species of *Procoptodon*.

Specimens of *S. pales* are considerably larger than those of any other species of *Sthenurus* yet located in the Upper Cainozoic deposits of Queensland. While associated maxillary and mandibular fossils have not been located, the mandible is referred to the species from consideration of the size and proportions of the teeth.

P^3 in *S. pales* is structurally similar to that of *S. atlas* as figured by Anderson (1932, fig. 5) but differs greatly in its relative proportions, being somewhat longer and much wider, and the ornamentation of the lingual basin appears to be more pronounced. The lower molars are comparatively wider across the trigonid basin than in *S. oreas*; and the accessory ridges on the antero-lingual surface of the hypolophid are all approximately equally developed, in contrast to the condition generally prevailing in this species, where the accessory ridge closest to the mid-link is dominant. Furthermore, the transverse ridge across the lingual moiety of the anterior cingulum is less clearly defined than in other species. Glauert (1910b) stated that *S. pales* is much larger, but resembles *S. occidentalis* in the arrangement of the accessory ridges on the anterior surfaces of the lophids and in the sculpturing of the posterior surfaces.

The maxillary specimen, Australian Museum number F. 16489, figured by Krefft (1882, pl. 10, fig. 11) as *Halmaturus* sp., is readily referable to *S. pales* by both structure and size. The fossil is from an unspecified Queensland locality.

STHENURUS ANTIQUUS sp. nov.

(Figures 9–10)

Sthenurus pales De Vis (*partim*), 1895, Proc. Linn. Soc. N.S.W., 10 (n.s.), pp. 94–96, pl. 15, fig. 3.

Sthenurus oreas De Vis (*partim*), 1895, Proc. Linn. Soc. N.S.W., 10 (n.s.), pp. 96–97, pl. 16, figs. 7–8; Anderson, 1932, Rec. Aust. Mus., 18, p. 386.

" *Sthenurus* " *oreas* Stirton, 1957, Mem. Nat. Mus. Vic., 21, p. 124.

MATERIAL.—F. 2975, holotype, partial left maxilla with P^3–M^2, ?Chinchilla, Darling Downs (figd. in part, De Vis, 1895, pl. 16, figs. 7–8).

F. 2973, partial left mandibular ramus with M_2–M_4, ?Chinchilla, Darling Downs; F. 2931, partial left mandibular ramus with P_3, M_1–M_4, Darling Downs including P_3 originally F. 2932 (figd. De Vis, 1895, pl. 16, fig. 3), now tentatively associated with F. 2931; F. 2974, partial right mandibular ramus with M_3, Darling Downs; F. 3818, right P_3, south-eastern corner of Chinchilla Rifle Range (Rifle Range No. 78, parish of Chinchilla), Darling Downs; F. 2976, partial right maxilla with M^1–M^3, Darling Downs; F. 2977, partial left maxilla with M^2–M^3, Darling Downs; F. 3387, partial right maxilla with M^3, Darling Downs; F. 3816, partial left M^2, Chinchilla Rifle Range.

DIAGNOSIS.—Short-jawed; ramus relatively wide, with longitudinal axis slightly convex laterally; masseteric crest low, raised only to level of accessory foramen. P_3 elongate, moderately coarsely ornamented. Lower molars with wide, low, rectilinear lophids, with very reduced ornamentation on anterior and posterior surfaces; trigonid basin moderately wide. P^3 moderately elongate, posteriorly broad, moderately ornamented, lacking a postero-labial fossette; lingual crest relatively low. Upper molars with somewhat anteriorly bowed lophs, with reduced but distinct ornamentation; anterior cingulum broad.

Measurements

Mandible

Specimen	P_3	M_1	M_2	M_3	M_4	Mandible depth and width below M_2–M_3
F. 2931	17·6 x 10·0	14·5 x —	16·5 x 12·6	16·6 x 12·9	15·8 x 12·6	30·2 x 18·5
F. 2973	——	——	14·9 x 11·5	16·1 x 12·2	15·5 x 12·3	— x 17·5
F. 2974	——	——	——	16·4 x 12·4	——	——
F. 3818	— x 9·1	——	——	——	——	——

Description.—I_1, P_2, and DP_3 unknown.

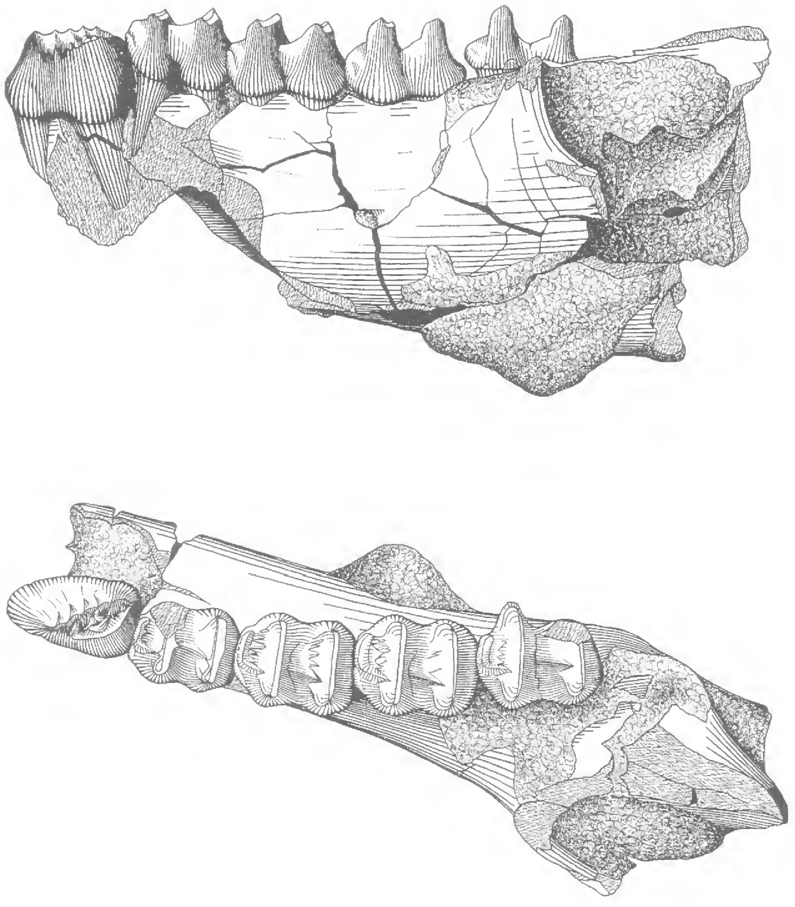

Figure 9.—*Sthenurus antiquus* sp. nov. Lateral and occlusal views of incomplete mandible; F. 2931, natural size.

Mandible strong, relatively wide, comparatively shallow, with longitudinal axis slightly convex laterally. Accessory foramen well-defined, halfway between anterior root M_3 and ventral margin of ramus. Ventral margin of ramus rounded; diagastric process postero-ventral to M_4, weakly developed; bounded above by shallow diagastric fossa; this fossa separated above from shallow depression opening posteriorly into pterygoid fossa. Post-alveolar shelf moderately long, leading to post-alveolar ridge, ascending gradually posteriorly. Masseteric crest raised approximately to level of accessory foramen.

P_3 elongate, robust, subtriangular in basal outline, with cingulum-like structure anteriorly at basal margin ; longer than any molar. High lingual crest, markedly concave lingually, transected by three sets of vertical ridges with production of well-defined cuspules along crest ; high, curving, postero-labial crest, flanked anteriorly by insignificant groove and mesially by small fossette ; intervening basin coarsely ornamented by ridges and tubercles.

$M_1 < M_2 < M_3 > M_4$; molars subrectangular, slightly constricted across talonid basin ; lophids low, rectilinear, with hypolophid broader than protolophid in M_1, but protolophid broader in other molars, and extremely so in M_4. Trigonid basin relatively broad, short, its length being approximately three-fifths distance between lophids ; fore-link extremely low, slight, descending lingual to and well below level of protoconid, anteriorly to near mid-point of anterior margin, then turning abruptly lingually as slightly curving transverse ridge above low anterior cingulum ; accessory ridges on anterior surface of protolophid very weak, few, but variable ; oblique ridges from protoconid and metaconid well-defined ; posterior surface very weakly ridged. Hypolophid with mid-link low, very weak, descending lingual to and below level of hypoconid anteriorly across elevated central portion of talonid basin to near mid-point of posterior surface of protolophid ; accessory ornament of oblique ridges from hypoconid and entoconid, and few extremely weak ridges lingual to the mid-link ; posterior surface very finely ridged. Posterior cingulum ill-defined.

Measurements

Maxilla

Specimen	P^3	M^1	M^2	M^3
F. 2975, holotype ..	15·2 x —	13·6 x 12·3	14·9 x 13·7	——
F. 2976	——	12·4 x —	14·5 x 12·0	15·3 x 12·3
F. 2977	——	——	15·3 x 13·6	15·4 x 13·8
F. 3387	——	——	——	16·0 x 13·8

I^{1-3}, P^2, DP^3, and M^4 unknown.

P^3 moderately large, elongate, broader posteriorly. Crown with high, slightly concave labially longitudinal crest, transected by three sets of vertical ridges, with production of cuspules at crest. Low lingual crest curving and descending in its anterior and posterior extensions from protocone and hypocone ; crests separated by shallow basin, crossed by several moderately coarse ridges.

$M^1 < M^2 < M^3$; molars subrectangular, slightly constricted across median valley ; lophs low, slightly anteriorly bowed ; metaloph broader than protoloph in M^1, protoloph broader in M^2 and M^3. Anterior cingulum low, short, moderately broad, ascending labially, bounded by small style ; protoloph anteriorly with very slight ridges passing to base of anterior cingulum. Median valley bounded labially by strong ridge descending from paracone and weaker ridge from metacone. Mid-link weak, low, descending postero-labially then posteriorly from a point labial to and below level of protocone. Enclosed portion of median valley ornamented by weak, but variable ridges from posterior surface of protoloph and, to lesser degree, anterior surface of metaloph. Posteriorly, oblique ridges from hypocone and metacone unite at posterior margin, limiting large, very broad posterior fossette, ornamented by reduced, but variable vertical ridges from below crest of metaloph.

All specimens here referred to *S. antiquus*, with the exception of the P_3 now associated with F. 2931, F. 3816, and F. 3818, were formerly included in *S. oreas* by De Vis (1895). F. 3816 and F. 3818 were recently collected, while the mandibular fragment with P_3, originally figured as *S. pales* by De Vis (1895, pl. 15, fig. 3), has been tentatively associated with F. 2931, because of their similarity of preservation and the near perfect correspondence of their broken surfaces. Since occlusion is satisfactory and the ornament of upper and lower molars is correspondingly reduced, it is felt that the mandibular remains have been correctly referred. However, this has not been confirmed by field association.

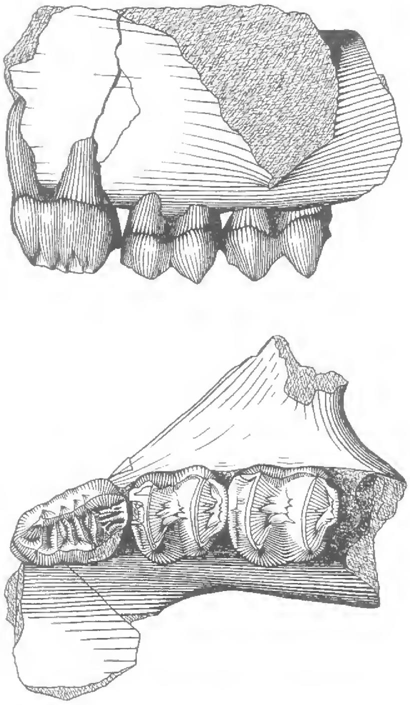

Figure 10.—*Sthenurus antiquus* sp. nov. Lateral and occlusal views of maxillary fragment; F. 2975, holotype, natural size.

F. 2976, a maxillary fragment originally referred by De Vis (1895) to *S. oreas*, is slightly smaller than specimens of *S. antiquus* and differs by lacking a pronounced labial ridge from the metacone into the median valley. However, since occlusion is unsatisfactory between this specimen and the poorly preserved mandibular material believed to be from the Chinchilla Sand and discussed previously with *S. andersoni*, association with this appears unlikely, and the specimen is thought to be only an extreme variant of *S. antiquus*, but its reference must remain doubtful until additional material is collected.

S. antiquus is closely allied to *S. oreas* from the Pleistocene, a fact obvious from comparison of both maxillary and mandibular remains. The ramus in *S. antiquus* is slightly narrower, but has a somewhat similar convexity of the longitudinal axis. The accessory foramen is positioned more posteriorly in specimens of approximately the same stage of tooth eruption and the masseteric crest, being raised to near the level of the accessory foramen, is at a much lower level than in *S. oreas*. The lower molars in *S. antiquus* are considerably larger and exhibit a much reduced ornamentation, with the most notable structural contrast being the absence of the very strong accessory ridge on the anterior surface of the hypolophid between the mid-link and the lingual margin. Although the trigonid basin is relatively broad in *S. oreas*, it is broader in *S. antiquus*. If the association of P_3 is correct, then the unusual condition prevails in this species whereby the length of this tooth exceeds that of its upper counterpart. Similarly, *S. oreas* and *S. antiquus* could be readily separated on the size of P_3. The third upper premolar has not yet been located in *S. oreas*, but the upper molars in that species are again smaller and possess somewhat similar but much more accentuated ornamentation.

Anderson (1932) listed the maxillary fossil now constituting the holotype of *S. antiquus* as *S. oreas* (under its original catalogue number, 11204), and compared the specimen with *S. occidentalis* and *S. atlas*. He noted that the permanent upper premolar is similar in form to that of *S. occidentalis*, but is smaller, while the upper molars are about the same size, or may be larger than those of *S. atlas*. Like those of *S. occidentalis*, the upper molars have accessory ridging. De Vis (1895) stated that the present specimen fits exactly the type of *S. oreas*, a statement which is incorrect, the occlusion in reality being poor.

All the specimens in the Queensland Museum collections, definitely referred to *S. antiquus*, are believed to have been collected from the Chinchilla Sand of possible Pliocene age, at Chinchilla, but one mandibular specimen, figured by Owen (1874, pl. 22, fig. 9; pl. 24, figs. 7–8) as *S. atlas*, is from Gowrie, from the Pleistocene fluviatile deposits of the Darling Downs (*fide* Lydekker, 1887). This appears to be structurally similar to *S. antiquus* and is possibly referable to this species.

STHENURUS NOTABILIS sp. nov.

(Figure 11)

MATERIAL.—F. 3817, holotype, partial right mandibular ramus with P_2–M_1, P_3 excavated, western side of large gully system, Chinchilla Rifle Range, (Rifle Range No. 78, parish of Chinchilla), Darling Downs.

DIAGNOSIS.—Moderately short jawed; ramus wide, with longitudinal axis slightly convex laterally; mental foramen small. P_3 elongate, wider posteriorly, with lingual crest transected by three sets of vertical ridges, with the production of cuspules along the crest; postero-labial crest high, separated from lingual crest by deep, relatively coarsely ornamented basin. Molars with extremely high, rectilinear lophids, each with accessory ridge closest to link moderately well developed; links strong, high, with fore-link ornamented by slight ridges; trigonid basin narrow; lateral surfaces of lophids only slightly convex in anterior view.

Measurements

Mandible

Specimen	P_2	DP_3	P_3	M_1
F. 3817, holotype ..	10·6 x 8·5	13·0 x 9·9	16·7 x 9·8	17·0 x 12·2

DESCRIPTION.—I_1, M_2–M_4 are unknown, but the alveolus of the incisor suggests that it was a large tooth, set at a moderate angle to the base of the ramus.

P_2 small, robust, subovate in basal outline, slightly constricted mesially; lingual crest transected by two sets of vertical ridges with production of cuspules at crest; curved postero-labial crest flanked anteriorly by broad groove extending to base of crown; intervening basin moderately deep, ornamented.

DP_3 molariform, subrectangular in basal outline, constricted across talonid basin, with very high rectilinear lophids; hypolophid broader than protolophid. Trigonid basin moderately narrow and short, its length being approximately three-fifths distance between lophids. Fore-link strong, high, descending antero-lingually from near protoconid then anteriorly to near mid-point of low anterior cingulum, then turning abruptly lingually as curving transverse ridge; oblique ridge from metaconid descending into trigonid basin. Hypolophid with strong, high ridge descending antero-lingually from below crest near hypoconid, across centrally elevated area of talonid basin to near mid-point of posterior surface of protolophid; accessory ornament of oblique ridges from hypoconid and entoconid and single, moderately coarse ridge just lingual to mid-link. Tooth base swollen posteriorly into cingulum-like structure, broadly elevated centrally into low ridge.

P_3 moderately long, robust, subtriangular in basal outline, broader posteriorly. Lingual crest transected by three sets of vertical ridges with production of cuspules at crest; prominent, high, curved postero-labial crest flanked anteriorly by deep groove extending towards base of crown; intervening basin deep, relatively coarsely ornamented, mainly from postero-labial crest. Base of crown slightly swollen anteriorly.

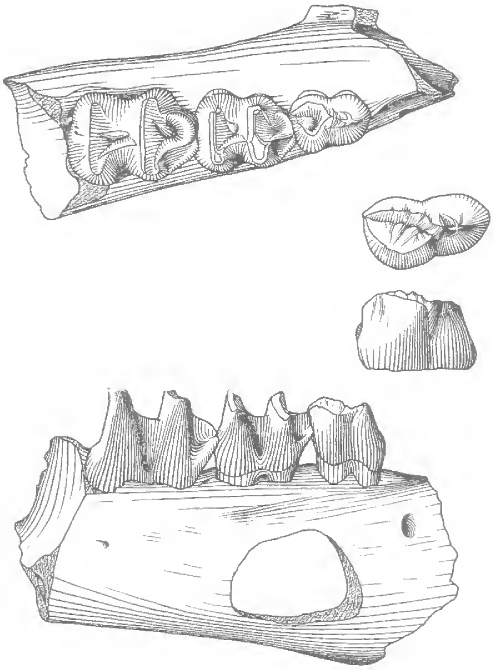

Figure 11. *Sthenurus notabilis* sp. nov. Occlusal and lateral views of incomplete, juvenile mandible, with unerupted P_3 exposed by fenestration; F. 3817, holotype, natural size.

M_1 subrectangular, constricted across talonid basin; lophids rectilinear, extremely high, with height of hypolophid above tooth base being approximately four-fifths length of tooth; hypolophid slightly broader than protolophid. Trigonid basin narrow, its length approximately equalling distance between lophids. Fore-link strong, high, ornamented by slight ridges, descending lingual to and below level of protoconid, anteriorly to near mid-point of anterior margin then turning abruptly lingually as strongly curved transverse ridge above low anterior cingulum; anterior surface of protolophid ornamented by single accessory ridge just lingual to fore-link, and by oblique ridges from protoconid and metaconid. Posterior surface only very weakly ridged. Hypolophid with mid-link high, strong, descending across centrally elevated portion of talonid basin lingual to and below level of hypoconid to point labial to mid-point of posterior surface of protolophid; accessory ornament of oblique ridges from hypoconid and entoconid and one relatively strong ridge just lingual to the mid-link. Posterior surface faintly ridged. Tooth base swollen posteriorly into cingulum-like structure, broadly elevated mesially into low ridge.

Although *S. notabilis* is known only from a single specimen, it can be readily separated from other species of *Sthenurus*. A consideration of the relationship of the two genera suggests that species of *Sthenurus* showing closer resemblances to *Procoptodon* are liable to be encountered in older sediments. This is the case with this species where there is an increase in the degree of ornamentation of the posterior surface of the hypolophid and the fore-link, and where the lateral tooth margins exhibit reduced convexity in anterior view. However, generic characters diagnostic of *Sthenurus* are clearly exhibited. The form does not fit into either the long or short-jawed groups of *Sthenurus* suggested by Marcus (1962), the ramus being like those of the short-jawed species, while the cheek teeth are generally more similar to those of the long-jawed group.

P_3 is not as elongate relative to the lengths of the anterior molars, as in other species of *Sthenurus*, apart from *S. oreas*. Morphologically it shows some resemblance to that of the type of *S. atlas*, figured by Owen (1838, 1874), and approaches even more closely the isolated specimens of P_3 tentatively referred to *S. antiquus*. However, it has a more complicated oblique crest and a less ornamented postero-labial basin. The most significant feature of the molariform teeth is the great height of the lophids. The molars are larger than those in *S. atlas* and are relatively uncomplicated by accessory ridging, there being only one moderately strongly developed accessory ridge on each lophid. In the ornamentation into the talonid basin, *S. notabilis* appears somewhat similar to *S. oreas*, although in that species there are numerous equally developed minor ridges associated with the protolophid.

DISCUSSION

Woods (1958, 1960b, 1962) had indicated that the diprotodontid fauna of the Chinchilla Sand, of possible Pliocene age, in the north-western Darling Downs, is different from that of the Pleistocene fluviatile deposits in the south-eastern Darling Downs, while Woods (1956) and Bartholomai (1962) have shown the presence of two related species of *Thylacoleo* Owen, from the same areas.

A similar condition exists with regard to the species of *Sthenurus* Owen, where *S. andersoni* and *S. pales* are restricted to the Pleistocene fluviatile deposits, and in addition *S. oreas*, present in these alluvia, has also been collected from the fissure-fill material of Pleistocene age at Cement Mills, Gore, south-eastern Queensland. On the other hand, *S. notabilis* and *S. antiquus* appear to be restricted to the Chinchilla Sand, with the possible exception of one specimen of the latter species in the British Museum (Natural History) collections. Other fragmentary material, presumably from the Chinchilla Sand, may indicate the presence of an additional small ?Pliocene form of *Sthenurus*. *S. atlas*, which was previously recorded from the Queensland Upper Cainozoic sediments by De Vis (1895) and Owen (1845, 1874), is now considered to be totally lacking.

The revision of the genus is based solely on cranial specimens, and no attempt has been made to associate postcranial fossils. Apart from the one record of *Sthenurus* from fissure-fill deposits, all specimens are derived from sediments which appear to be of fluviatile origin. This limits the possibility of locating associated cranial and postcranial remains, because of the disarticulation and scattering of skeletal elements generally prior to preservation.

Marcus (1962) suggested that *S. atlas* and *S. andersoni* may be regarded as long-jawed members of the genus, while *S. oreas*, *S. pales* and *S. occidentalis* are short-jawed, being more like *Procoptodon* in this respect. *S. antiquus* is readily associated with the short-jawed forms, but *S. notabilis* cannot be neatly associated with either group. Because of the presence of such a species as *S. notabilis*, a subgeneric distinction between the long-jawed and short-jawed species of *Sthenurus* has not been proposed. The phylogenetic relationship between *S. oreas* and *S. antiquus* appears to be linear, with *S. oreas* being directly descended from the ?Pliocene *S. antiquus*, and exhibiting a notable increase in complexity of the molar ornament.

The structural characters which indicate the aberrant nature of *Sthenurus* as a macropodine genus appear to be due to a secondary reversion to the browsing habit. Ride (1959) has shown that this was the case with *Procoptodon*, a genus apparently derived from primitive *Sthenurus* stock, late in the geological history of the group. This reversion, however, was never as complete as with species of *Procoptodon*, although approaching it in some respects in the short-jawed forms. It is implied that this trend to the browsing habit developed at least along two distinct lines.

SUMMARY

A study of all available specimens relating to the occurrence of the genus *Sthenurus* Owen in Queensland has resulted in the revision of *S. oreas* De Vis and *S. pales* De Vis, the description of two new species, *S. antiquus* and *S. notabilis*, and the recognition of the extension of the range of *S. andersoni* Marcus.

Of the species at present recognized, *S. andersoni*, *S. oreas* and *S. pales* are from the Pleistocene fluviatile deposits, while *S. antiquus* and *S. notabilis* appear to be restricted to the Chinchilla Sand, of ?Pliocene age.

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